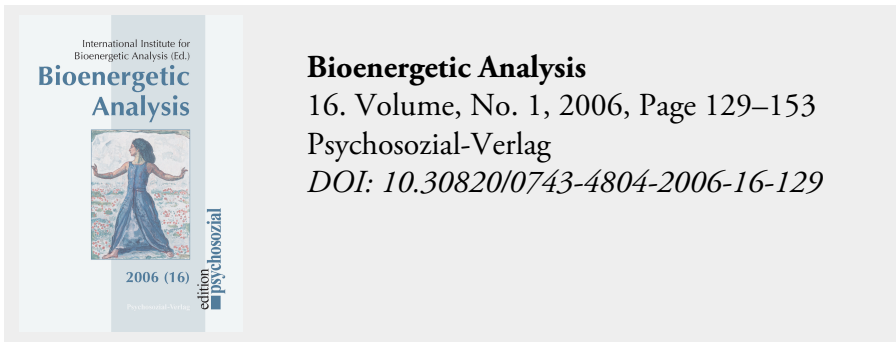


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Explorations into the Neurological Basis of our Sense of Self



Bibliographic information of Die Deutsche Nationalbibliothek (The German Library)
The Deutsche Nationalbibliothek lists this publication in the Deutsche Nationalbibliografie;
detailed bibliographic data are available at <http://dnb.d-nb.de>.

2006 Psychosozial-Verlag GmbH & Co. KG, Gießen, Germany
info@psychosozial-verlag.de
www.psychosozial-verlag.de



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Cover image: Ferdinand Hodler *Ausschreitende Frau*, 1910, oil on canvas, 48,5 x 39 cm

<https://doi.org/10.30820/0743-4804-2006-16>

ISBN (PDF-E-Book) 978-3-8379-6879-8

ISBN (Print) 978-3-89806-517-7

ISSN (Online) 2747-8882 · ISSN (Print) 0743-4804

Explorations into the Neurological Basis of our Sense of Self¹

Anton Lethin

Summary

The sense of self as a covert agent is a key component to the sense of self. This paper focuses on covert action as a preparation to interact. This activates the entire motor system, including the gamma motoneurons innervating the muscle spindles. The proprioceptive stimulation is fed back to the network of origin, contributing to a sense of self as generating the covert activity.

A study of motivated behavior in the rat is presented to clarify how the motivation potentiates actions in the body. This is set into Panksepp's subcortical action system of emotional circuits, where the motivation arises. This sets the motor tone for the planned action.

This picture is interpreted with Ellis's and Newton's model portraying how emotional motivation can lead to phenomenal consciousness. It is proposed that no motor imagery occurs without involving the body. The higher levels of awareness depend on the subcortical bodily intentionality.

Key words: periaqueductal, covert, gamma, facilitation, somatosensory.

What is the connection between movement and feelings? Alexander Lowen says »feelings are the perception of an internal event«. What is this event? How do we experience it? How do we create it? »What is perceived is a movement. It is the basis of all active techniques that the ›I‹ includes not only the perceptions, but also those internal forces, Freud's ›undetermined elements‹ which give rise to perception.«

I propose that this internal event is an urge, a preparation to move by a covert agent. »The emotions are bodily events; they are literally movements or motions within the body that generally result in some outward action« (Lowen 1975, p. 55.). »These internal movements represent the body's motility as distinguished from the voluntary motions that are subject to conscious control« (ibid, p. 53).

1 Revised version of: Lethin A (2005a).

The following paper attempts to portray how the emotions are covertly activated in the body as demonstrated in experimental studies in neuroscience and psychology. It provides a partial framework for explaining some of the experiences developing in Bioenergetic analytic therapy. My own experience in Bioenergetic therapy and as a Bioenergetic therapist helped me to develop this view of covert activity.

The sense of self as agent is a key component to the sense of self. There is evidence that this depends on events preceding action that prepare for movement (Haggard & Libet 2001, pp. 47–63). It is now realized that actions involve a covert stage. »The covert stage is a representation of the future, which includes the goal of the action, the means to reach it, and the consequences on the organism and the external world« (Jeannerod 2001, p. S103). Does the sense of self depend on feedback from this covert activity? A sense of self as covert agent? If so, what is the nature of this feedback? This paper proposes that this covert preparation for an interaction with the affordance leads to somatosensory feedback from the body, and that this is necessary for a sense of self grounded in the body and the world. I believe this preparation is emotionally motivated.

Gallagher discusses a minimal self – »a pre-reflective point of origin for action, experience and thought (...) a consciousness of oneself as an immediate subject of experience, unextended in time. The minimal self almost certainly depends on brain processes and an ecologically embedded body (...)« (Gallagher 2000, p. 15). There are »two closely related aspects of minimal self-awareness: self-ownership – the sense that it is my body that is moving; and self-agency – the sense that I am the initiator or source of the action. (...) experimental research on normal subjects suggests that the sense of agency is based on that which precedes action and translates intention into action« (ibid, p. 16; my emphasis). This would include planning and preparing to act. The feedback from this to the network of origin leads to self-awareness.

Libet and Haggard, in separate experiments, showed that electroencephalographic events precede the conscious awareness of deciding to move (Haggard and Libet 2001, pp. 47–63). Haggard introduced a new element by including situations wherein a subject must choose between a left- and a right-handed action. »Since the motor system must have selected which specific movement to perform by the time that the readiness potential lateralizes, we concluded that conscious intentions were related to specific rather than general preparation for action« (Haggard & Libet 2001, p. 51). Their finding suggests that awareness of intention is associated with this lateralized readiness

potential, a stage of action preparation known to be devoted to the selection of the specific movement to be made.

What is the nature of this preparation? I want to focus on the preparations to move the body.

Bodily Intentionality

I would describe this as a bodily intentionality (Lethin 2002). »It is my body as a sensorimotor organism perceiving and acting in the world that *first* expresses intentionality. There is a bodily intentionality, on Merleau-Ponty's view, on which all other forms of intentionality rest« (Wider 1997, p. 135). I would suggest that the body's *preparing to interact* expresses this intentionality. »(...) intention does not directly generate behaviour, rather it *modulates response activation within a system that is sensitive to environmental (bottom-up) factors as well as intention (top-down control)*« (Humphreys & Riddoch 2003, p. 203; emphasis added). Jeannerod discussed the stage of covert actions: »The hypothesis that the motor system is part of a simulation network that is activated under a variety of conditions in relation to action, either self-intended or observed from other individuals, will be developed. The function of this process of simulation would be not only to shape the motor system in anticipation to execution, but also to provide the self with information on the feasibility and the meaning of potential actions« (2001, pp. S103). Gallagher interviewed him and responded: »You suggest that goal-directedness is a primary constituent of action (...) This means, I think, that the motor system is not simply a mechanism that organizes itself in terms of what muscles need to be moved, but it *organizes itself around intentions*« (Gallagher & Jeannerod 2002, p. 13; emphasis added). The pre-movement activity identified by Jeannerod in the motor system represents bodily intentionality. This involves the whole organism in an integrated action – visual, autonomic including blood flow, neuropeptide, neurotransmitter, and hormonal changes. (Damasio 1999, pp. 145–9; Decety 1993, pp. 549–563).

Newton's definition of representation is similar to Jeannerod's definition of the covert stage: »Representation is the process of performing goal-directed activity in a manner that allows the activity to be rehearsed and optimized in advance of the realization of the goal. This realization (whether planned or simply hypothesized) is what is represented by the activity« (Newton 2004). She has moved beyond just including the goal in the planning of the action to providing for *rehearsal and optimizing*.

How can the organism rehearse and optimize an activity before the performance? In order to optimize this covert pre-movement activity, the organism will need afferent input from both the affordance and from the body. The organism needs to know what posture the body is starting from, and where the affordance is in relation to the body. The physiological system for proprioception involves the muscles and tendons, the visual apparatus, and the labyrinths of the inner ear. Based on these studies and others, Marcel radically proposed that what he calls »(...) a minimal sense of ownership is provided by the *spatial* content of movement specifications (...) The (...) body parts that are to implement the action must be specified in a common reference frame with the targets (...) The only spatial description *common for all body parts and for external locations* is an egocentric one (...) The self enters the representational scene as the origin of the egocentric frame of reference utilized in movement specification (...) This would give, in the normal phenomenology, a perspectivalness of the source of the action, that is, spatial points of origin and intention.« He views the experience of the self during action as being immersed, meaning that the self is perceptually recessive – there is no reflective consciousness of self (Marcel 2003, p. 43). Newton has a similar view: »While bodily awareness seems to be a background element in all conscious experience, it can and frequently does fall outside the focus of attention. In those cases we may be said to be conscious ›only‹ of external sensory input. But while we may speak in that way, the very notion of *externality* presupposes some awareness of one's own body and its boundaries, as does any awareness of possible interactions with the external world – its ›affordances‹« (Newton 2001, p. 57; original emphasis).

Neuromuscular Basis of Bodily Intentionality

I want to focus now on the neuromuscular aspect of bodily awareness. The activity in the brain can facilitate a movement by stimulating the gamma motoneurons in the spinal cord (Eldred 1953). These stimulate the muscle spindles in the skeletal muscles, which are tiny stretch receptors that also contain a tiny muscle. When a muscle is stretched, the spindles sense this and increase the proprioceptive afference to the alpha motoneurons and to the spinal cord and brain. (See Fig. 1). When the gamma motoneurons stimulate the spindles, the spindle muscles contract and increase the proprioceptive stimulation, just as though the muscles had been stretched. This strongly facilitates the alpha motoneurons to the muscles. See appendix for more

details. I call the loop from the brain to the gamma motoneurons through the spindles back to the brain the »body gamma loop«. The »peripheral loop« describes only the loop from the gamma motoneurons to the alpha motoneurons. How does this relate to preparing to move? Jeannerod investigated the relation of simulation of action to preparing to act. Functional brain imaging by magnetic resonance (fMRI) has shown activation of sensorimotor cortex during imagined action in multiple studies (Jeannerod 1999, p.8). Experiments on motor imagery supported »the *hypothesis that mental simulation of action is assigned to the same motor representation system as preparation to execution*« (ibid, p.4). If so, »mental simulation should activate motor pathways« (...) »The main result of this experiment was that motoneurons excitability, as tested by the amplitude of spinal monosynaptic reflexes, was increased during mental simulation (...) Insofar as the sensitivity of the neuromuscular spindles is under the control of gamma motoneurons, *the increase in excitability of the T-reflex, but not of the H-reflex, suggests a selective increase in gamma motoneuron activity during mental simulation of a movement*« (ibid, p. 7; emphasis added). T-reflex refers to the muscle stretch reflex when elicited by a tendon tap. H-reflex is a response to direct stimulation of the proprioceptive afferent fibers. Muscle stretch reflex results from the muscle spindles' stimulation of the alpha motoneurons. The muscles can be prepared to move by increasing the tension of the muscle spindles inside the muscles. This increases the proprioceptive afferent feedback both to the spinal cord and to the network originating the preparation of the body's readiness for the action (see below). Referring to Merleau-Ponty's emphasis on body intentionality and reflexivity, Wider quotes Dillon: »It is his ›discovery of corporeal reflexivity (...) (that is) the means to overcome ontological dualism« (Wider 1997, p. 138; Dillon 1993, p. 79).

Preparing to act is very complex. In my view it is a total preparation of the organism. This involves the autonomic nervous system, including hormonal, neurotransmitter, and neuropeptide changes (Damasio 1999, pp. 59–62). Even mental simulation of action activates cardiac and respiratory control mechanisms (Decety et al. 1993, pp. 549–563). They suggest that autonomic activation during imagined action is part of the more general phenomenon of preparation for action. It includes the entire nervous system. Even so, the motor preparation all ends up facilitating the alpha motoneurons to the muscles to be contracted and inhibiting the antagonists. Part of the facilitation is caused by the gamma motoneurons' stimulation of the muscle spindles (Lethin 2005 b).

Panksepp's Emotional Circuits

At this point it will clarify the proposition on preparation to transpose it to the network of emotional circuits described by Panksepp in his book (1998a). He has written in his seminal work summarizing decades of his and others' experimental studies about the seven basic motivational-behavioral systems that converge on the periaqueductal gray. I propose that the *covert preparation to interact originates here*. He believes these seven basic circuits are primitive networks that have persisted during evolution in mammalian brains, and are the roots of emotion in primitive »value generators«. Each system emphasizes a different combination of neurotransmitter pathways, and is highly reactive to modulation by neuropeptides. These all project to a diencephalic-midbrain area with an epicenter in the periaqueductal gray, and they are expressed by activating innate motor programs. Their »initial adaptive functions were to initiate, synchronize, and energize sets of coherent physiological, behavioral, and psychological changes« (ibid, p. 123). He emphasizes the role of motor functions: »In affective experience, a *direct motor preparatory linkage appears to be especially evident* (...) The intrinsic neurodynamics of such affective, *motor-tone setting circuits*, along with various converging somatic and visceral inputs, may create a pervasive and fractally propagated feeling of self-ness within the organism« (Panksepp 1998b, p. 574–5; emphasis added). This suggests that the sense of self as covert agent may originally have developed with the adjusting of motor tone as a movement is prepared. Motor tone is the tension in the muscles, and this can be perceived by the resistance, which a muscle offers to passive stretching. It is maintained by a low-frequency, asynchronous discharge of impulses in a small fraction of the motor nerve fibers supplying a muscle. It is dependent on the gamma motoneurons stimulating the muscle spindles (which facilitates the alpha motoneurons), and can be modulated by supraspinal facilitation or inhibition (Bard, 1961, pp. 1117–8) (see Fig. 1 in this paper). »In the present context, primary process intentionality is envisioned to be the natural action readiness that is intrinsically coded within the interaction of emotional processes with the neural representation of the SELF« (Panksepp 1998b, p. 573). This is an emotionally motivated preparation to move to interact with the affordance.

He uses the capitalized SELF to refer to this *fundamental neural substrate* as a distinct brain system as opposed to all the associated psychological states that coalesce during development. He refers to this as a »Simple Ego-type Life Force«. It is important to bring out the primary role he envisages for

this system. This »is the lowest region of the brain to orchestrate various coordinated emotional responses via a variety of motor outputs« (ibid, p. 570). In discussing the evolutionary development of this network, he concludes: »I assume the SELF provides the first executive mechanism for behavioral coherence and bodily awareness« (Panksepp 1998a, p. 311).

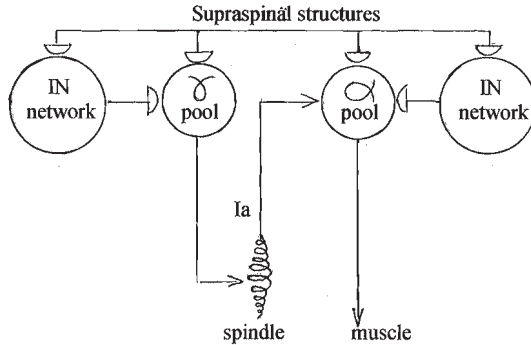


Fig. 1. Simplified diagram of the neural organization of the monosynaptic reflex. The gamma and alpha motoneuron pools are located in the spinal cord. The muscle spindle is imbedded in the skeletal muscle, but has no direct neural connection to it. Its proprioceptive Ia fibers project to the alpha motoneuron pool. IN indicates interneurons. Arrows show activating effects, whereas semicircles indicate possible activation or inhibition. (Adapted from a figure by Requin et al. 1977.)

Motivated Behavior in the Rat

His emphasis on *motor-tone setting as part of readiness* can be looked at more closely by using an example. I want to describe a study of motivated behavior in the rat to illustrate this view. Stellar's classic work proposed that the hypothalamus was the center of motivated behavior (Stellar, E. 1954, pp. 5–11). Pfaff did a thorough investigation of the neural pathway from the hypothalamus involved in the execution of the lordosis reflex in the female rat (Pfaff 1980, pp. 1–281; Stellar & Stellar 1985, p. 73). The rat was motivated to get ready for copulation by preparing to hyperextend her lower back. With

lordosis the female becomes sexually receptive to the male. They administered the estrogenic substance estradiol to the female rat to facilitate this reflex.

The pathway represents a convergence of hypothalamic influences on spinal cord reflexes via brainstem mechanisms. The output of ventromedial hypothalamic cells, excited by estradiol, converges on midbrain central gray neurons with afferent sensory input and on midbrain reticular formation neurons. From there, the descending influences are relayed through the reticular formation of the medulla and the lateral vestibular nuclei to ventral horn cells of the spinal cord via the lateral vestibulospinal and reticulospinal tracts. Here, between T-12 and S-1, the *reflexes of vertebral dorsiflexion are executed in response* to flank, rump, and perineal stimulation by the male rat. Thus lordosis and a sexually receptive posture are executed by the female rat (See Fig. 2) (Pfaff 1982, p. 290–2; Pfaff 1980, pp. 190–1, 239–41). The estrogenic stimulation of the hypothalamus does not elicit a lordosis reflex. It only prepares the rat to interact. The cutaneous stimulation either by the male rat or administered experimentally is necessary for lordosis to occur (Sakuma & Pfaff, 1979a, b).

I interpret the process as follows. The estrogenic stimulation has activated the latent innate goal to receive the male rat's advances. This motivates the preparation of the lordosis behavior by potentiating the muscles' contraction. This can occur by *tensing the spindle muscles* within the extensor spinal muscles. As this occurs, there is increased proprioceptive stimulation both to the alpha motoneurons in the spinal cord and back up to the brain stem and hypothalamus in the areas originating the preparation of the muscles (See Fig. 1). »Descending tracts might have either of two modes of action in facilitating lordosis. One is a tonic effect, in which spinal circuits relevant for lordosis would be *prepared* for reflex execution before the onset of the adequate peripheral stimuli. For instance, tonic facilitation might result in a subliminal amount of background activity in motoneuron pools which supply muscles important for lordosis and a corresponding reduction in activity in motoneuron pools for muscles antagonistic to lordosis. Against this prepared background, cutaneous stimuli adequate for lordosis would be able to trigger the behavioral response« (Pfaff 1980, p. 190; original emphasis). He goes on to describe a possible second mode of action, which would involve spinobulbospinal reflex loops, initiated by cutaneous afferent activity. This would not be a major mode of action.

Preparatory action occurs at several different levels. How does the motor image of the planned action arise? There is a hierarchical organization of the planned interaction, with source-schemas, component schemas, sequencing

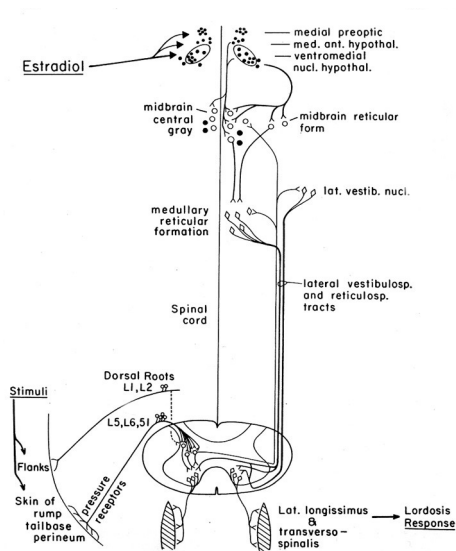
schemas and motor schemas representing different degrees of integration of the same action (Jeannerod 1997, p. 173).

»The hypothalamus is only part of an extensive limbic system involving the brainstem, diencephalon and forebrain. In many cases it may be the major integrator in a hierarchy of integrators along the neuraxis« (Stellar & Stellar 1985, p. 27). The »most immediate behaviorally relevant action would be at the lumbar spinal cord level. Preparatory action with a longer time course appears to take place in the lower brainstem. Some components of tonic facilitation may also occur in the central gray of the mesencephalon. Finally, the longest time course of cellular preparation for lordosis behavior must occur in and around the ventromedial nucleus of the hypothalamus, where long-acting estrogenic effects are registered« (Pfaff 1980, p.191). This picture of preparing for an action raises the question of *whether planning for an action at a high level can lead to the experience of self as agent*. Pfaff's work suggests that the preparation at the high level integrates the preparing at all the levels of the nervous system. This implies that the experience will be based on feedback to all levels of the self – from the periaqueductal gray to the prefrontal cortex. Gallistel pointed out that »(...) higher-level circuitry coordinates the activities of the lower circuits primarily by regulating their potential for activation, a phenomenon I term selective potentiation and depotentiation« (1980, p. 398). He finds that these processes of *potentiation and depotentiation are how motivational processes influence behavior*. On the spinal level the alpha motoneurons to the lateral longissimus and transverse spinalis muscles are facilitated. This can also be described as potentiated. The muscle contraction will be much stronger if and when it occurs. Any afferent stimulation from the appropriate cutaneous nerves will also directly stimulate both the gamma and alpha motoneurons as well as the central nervous system.

With the proprioceptive afferent feedback the rat experiences her motor intentionality to assume a lordotic posture in interaction with a male rat. Can we assume that she experiences the preparing with her self as the agent? The goal-oriented activity is sensed in the networks of origin, so that I believe we can assume that the rat feels this as an action of her SELF, as defined by Panksepp. The latent disposition to interact sexually with a male rat is innate, and obviously includes the goal. When this disposition is activated, the preparing to interact adjusts to this actual male rat moving now in this corner of this cage or room.

As mentioned above, the estrogenic stimulation of the hypothalamus does not elicit a lordosis reflex. It only *prepares the rat to interact*. The cutaneous

stimulation either by the male rat's mounting or administered experimentally is necessary for lordosis to occur. The female rat was *motivated* to lordotically interact with a male rat. The cutaneous stimulation would amplify the motivation and give it priority over other dispositions. In the report by Pfaff he did not describe the gamma motor stimulation to the muscle spindles. He interpreted the descending influences from the hypothalamus as being below the threshold for activating muscle contraction. »The parameters of motoneuron-muscle dynamics most clearly controlled by lateral vestibular and lateral reticular influences (for instance, »muscle stiffness« and the threshold for the stretch reflex ...) remain to be determined« (Pfaff 1980, p.206). The gamma motor activity and proprioceptive response could be studied directly in the female rat to confirm my interpretation. This is an example of how motor intentionality is embodied, which in this instance is activated by estradiol administration. The goal and motor program are innate.



Seeking System Activates Preparation

I want to place this lordosis »reflex« into the picture visualized by Panksepp. He proposes that the primitive self is based on a subcortical network which

is the primitive initiator and motivator for the organism. As mentioned above, this is in the diencephalon and mesencephalon centering in the periaqueductal gray, and with adjacent networks it integrates the emotional circuits, sensory input, motor activity, and autonomic nervous system. This network is responsive to the body's needs and functions like Damasio's proto-self (1999, p. 153–160).

The emotional-motivational circuits organize diverse behaviors by activating or inhibiting motor plans. One of these is the SEEKING system. He uses capitals to indicate that it refers to one of the genetically ingrained emotional operating systems. Previously he called this the »appetitive motivational seeking system which helps elaborate energetic search and goal-directed behaviors in behalf of any of a variety of distinct goal objects« (Panksepp 1998a, p. 52). »(...) the emotive tendencies aroused by this type of brain stimulation most clearly resemble the normal appetitive phase of behavior *that precedes consummatory acts*« (ibid, p. 147, my emphasis). Richard Depue called the seeking system the behavioral facilitation system (Depue 1989, p. 458). »(...) when fully aroused, it helps fill the mind with interest and motivates organisms to move their bodies effortlessly« (Panksepp 1998a, p. 52). As for subjective experience, he suggests »that ›intense interest‹, ›engaged curiosity‹, and ›eager anticipation‹ are the types of feelings that reflect arousal of this system in humans« (ibid, p.149). Watt points out that the seeking system »probably underpins a most basic emotional capacity (...) – the capacity to experience *hope*« (1999, p. 195). There are two components to this arousal. For example, when the organism espies and prepares to move toward the food nearby, his *experience of eager anticipation occurs without any movement*. Then when he starts moving toward the food, he can sense the movement with continuing eager anticipation of the consummation.

The seeking system is »quite motivationally and goal non-specific, facilitating only the relative activation of other potentially affectively rich interactions with others and the environment, mediated by activations of the other primes or prototypes, and of course, the hypothalamic mediation of homeostasis in the seeking of food, drink, and other biological requirements« (ibid, p. 196). One example would be the specialized neurons that are sensitive to the various hormones that control sexual tendencies, one of which is estrogen. When Pfaff administered estradiol to the female rat, this sexual urge was expressed through the SEEKING system. »Critical circuits that sensitize the lordotic spinal reflex via tonic descending influences arise from the central gray of the midbrain and the ventromedial hypothalamus (...)« (Panksepp 1998a, p. 240). *The most effective way to sensitize the spinal reflex*

is to increase the tension in the muscle spindles by stimulating the gamma motoneurons. The cutaneous stimulation affects the gamma and alpha motoneurons in the lumbosacral spinal cord, and this elicits a lordosis spinal reflex without needing further supraspinal involvement. As Depue said, the behavior is facilitated by the SEEKING system.

Panksepp points out that »the core of the SEEKING system is remarkably well highlighted by the trajectory of brain DA systems, especially the mesolimbic and mesocortical components which ascend from the A10 DA neurons of the VTA to the shell of the nucleus accumbens, and areas of the frontal cortex and amygdala« (ibid, p. 156). (DA refers to dopamine and VTA to ventral tegmental area in the mesencephalon). The energizing aspects of dopamine are well documented. He adds, however, that the ascending DA systems are only one link within the complex chains of electrophysiological and neurochemical events, and it is certain that the system also has important descending components. The reticulospinal tract would be one of these.

Emotionally Motivated Preparing to Interact

We are phenomenally conscious of our sense of self as agent. Ellis and Newton proposed a characterization of consciousness, taken from their phenomenal experience of it, which they broke down into three elements (Ellis & Newton, 1998, p. 439). I want to apply each of these to the lordosis reflex viewed in Panksepp's seeking system.

1. »An emotional motivation which grounds an interest in anticipating the future.«

The SEEKING system is one of the seven basic emotional systems of Panksepp. Even though this has not been considered such in the past, Panksepp's extensive research has demonstrated that it fulfills his criteria for the definition of an emotion. The hypothalamic stimulation of the SEEKING system in our example activates the motivation for the preparation. As mentioned above, the experience of the SEEKING system being activated can be described as one of eager anticipation. The anticipation facilitates the lordosis response when the affordance appears. The female rat is emotionally motivated to copulate with a male rat, and seeks this interaction. The motivation grounds the interest as it embodies it.

2. »Sensory, sensorimotor or proprioceptive imagery (which, by itself, can occur preconsciously) activated by this emotional motivation.«

Ellis and Newton emphasize that it is the emotionally motivated anticipation of input that leads to such »imagery«. They describe an image as „the felt sense that one is looking for (or listening for, tasting for, proprioceptively feeling for, etc.) some object or state of affairs that would take the form of an intentional object. The role of imagery in action-planning involves forming (not necessarily a visual or auditory image but) a sensory *and/or* proprioceptive *and/or* sensorimotor image of *oneself performing the action in the way planned*“ (Newton 1996; Ellis & Newton, 1998, p. 435; emphasis added). The image is representing »not just sensory data, but also the execution of bodily actions« (Ellis & Newton 1998, p. 436).

I want to focus on the process of »forming« in their description of imaging. It would appear that this is part of intentionality, since it involves seeking an intentional object. One aspect of this would be the motor intentionality that includes preparing a movement interaction with the affordance. If we look at the rat's motivation as potentiating the action at many levels, then this would take place in the experiment described in the hypothalamus and descending through the midbrain and brain stem to the spinal cord. To prepare to hyperextend the lower back would include stimulating the gamma motoneurons in the spinal cord, according to my hypothesis. This results in proprioceptive feedback from the muscle spindles, creating a proprioceptive pattern of the planned bodily action. Can this be described as the felt sense that one is »proprioceptively feeling for« a state of affairs (receiving the male rat)? This assumes that the pattern of gamma motor stimulation persists in memory. Then when the afferent proprioceptive pattern returns to the network of origin, the self can sense that one is seeking this state of affairs. There is reflexive self-reference. This can occur pre-consciously, as Ellis and Newton say. »To image something is to have an internally generated experience similar to the actual perceptual experience of that thing« (ibid, p. 439). The generating is the expression of intentionality. The female rat may also form a visual image of the male rat as part of the seeking, as well as an olfactory image and a cutaneous image. She is »looking for« a specific state of affairs. Searle has proposed that visual experiences have intentionality (Searle 1992, p.195), and I agree. There is an expected pattern that is prepared for, which may be pre-conscious. The intentional object mentioned above assumes the goal is part of the preparation to interact. To adjust the preparation to fit the goal requires that the sensory input from the affordance is integrated with the proprioceptive input and the efferent preparatory activity.

3. »A resonating between the activity of emotionally-motivated imagery and the activity stimulated by incoming sensory data and data reactivated through memory.«

Here we move to a higher level. »This core system of the SELF interacts closely with other nearby components for exteroceptive consciousness such as the Extended Reticular and Thalamic Activating System (ERTAS) (...) Thus, the PAG-centred emotional SELF system may be seen as the very core of the visceral-hypothalamic-limbic axis (which is essential for affective, interoceptive consciousness), while the ERTAS is the core of the adjacent somatic-thalamic-neocortical axis (which is essential for exteroceptive consciousness)« (Panksepp 1998b, p. 571). »PAG may even be essential for the arousal or maintenance of a conscious state, or at least for virtually all behavioural intentionality (...)« (Watt 1999, p. 196). As the estradiol-stimulated female rat is seeking to copulate with a male rat, she forms a proprioceptive image of the sought interaction. Then she sees and smells a male rat in the room. The sensory data from the male rat elicits a new instant of preparing to copulate, anticipating the future. The preparing of the motor interaction enables the perception. At the same time remembering previous copulation reactivates a latent disposition to copulate. These both interact with the emotionally-motivated imagery of copulating existing in its seeking activity. As Newton describes it, the past, present and future are blended. There is temporal thickness, and phenomenal consciousness emerges (Newton 2001, pp. 54–55). This is awareness of the experience, and does not imply any reflective consciousness.

Higher Levels Depend on Lower

Where does the experience of motor intentionality take place? It is controversial as to whether this occurs solely in the mind/brain, or in a brain-body-brain loop. For example, does the *preparation* to move generate directly the ›as-if sensation‹ of proprioceptive activity in the brain – proprioceptively ›imaging‹ what it would feel like to move in this way? Alternatively, does the organism prepare the entire body to move in a way that generates proprioceptive activity from the muscles themselves, as well as the rest of the organism? Looking first at high-level activity, I turn to Newton's description: »So what I'd say is that the intentional experience of planning (or just thinking about) an action with oneself as the agent, IS the experience of sensori-motor/proprioceptive goal-oriented activity. In that activity, the goal is part of the activity; forming action

images or high-level representations of that activity for planning purposes is being an agent« (Newton 2003). What is the *experience* of sensori-motor/proprioceptive goal-oriented activity? One imagines the activity (e.g., reaching to grasp an object in front of you), forming a dynamic pattern of the movement, including the expected proprioceptive and sensory feedback. Is this reflexive self-referring on a high-level? Is it somehow dependent on lower levels? »Although a high level of awareness is certainly not a local property of the PAG itself, such functions may emerge from the higher brain areas that are recursively linked to the PAG, especially in cingulate, frontal, and temporal lobes« (Panksepp 1998b, p. 578; PAG refers to the periaqueductal gray). There are supporting studies by Damasio 1994, Mantyh 1982, and Sesack et al. 1989). »Obviously, affective feelings, as all other forms of consciousness, are hierarchically organized in the brain, with *the higher functions being decisively dependent on the integrity of the lower functions*, but not vice versa« (Panksepp 1998b, p. 578; emphasis added). He summarizes evidence from studies with several approaches to validate his conclusion. The rat's preparing to hyper-extend her lower back is part of an affective feeling, part of the primitive emotional circuitry. The emotional motivation toward a specific goal activates the preparation for a movement interaction. The higher levels influence the selection and modulation or the inhibition of the lower levels, but this activity is all organized toward the goal generated in the subcortical area.

Ellis and Newton agree: »From an empirical standpoint, afferent processing, e.g., in the occipital lobe, never results in conscious awareness of the object unless accompanied by corticothalamic loops *instigated by midbrain motivational activity*, especially frontal-limbic activity« (Ellis & Newton 1998, p. 433; emphasis added; Posner & Rothbart 1992). As Merleau-Ponty has said, all higher levels of intentionality are dependent on a basic motor intentionality. This is where the motivation toward the goal arises. The prefrontal cortex may integrate and control the behavior, but the impetus toward the behavior comes from the PAG. »Eager anticipation and intense interest« describe the experience when the seeking system is aroused.

Proprioceptive Imaging

Can there be proprioceptive images created in the mind/brain without involving the body itself? »This imagining of action affordances is facilitated by the motorically-initiated efferent brain commands that Damasio calls the »as if body loop« (Ellis 2000, p. 45). This »as if body loop« bypasses the

body. Damasio has »suggested, and LeDoux agrees, that some emotional responses can change somatosensory representations in the brain directly, »as if« the latter were receiving signals from the body, although in effect the body is bypassed. People probably have both body-loop and as-if-body-loop mechanisms to suit diverse processing conditions. *The critical point, however, is that both mechanisms are body-related*« (Damasio 1997, p. 141; Damasio 1999, pp. 280–1; emphasis added). The body loop as described by Damasio did not specifically include a brain-gamma motoneuron-muscle spindle-proprioceptive afference-brain loop. I propose that this is part of the body loop.

Naito and colleagues investigated whether motor imagery contains kinesthetic sensations which are a substitute for the sensory feedback that would normally arise from the overt action (Naito et al. 2002, pp. 3683–3691). They induced an illusion of palmar flexion by vibrating a wrist extensor at a frequency known to stimulate the muscle spindles. They found that motor imagery of wrist movement influenced this sensory experience of kinesthetic illusion. They found »no peripheral inputs or minimal inputs, if any« during the motor imagery. They based this finding on the PET scans measuring regional cerebral blood flow. *Also they found no EMG activity during imagery*. This contrasts with some studies mentioned below. They did train their subjects to image without producing any EMG activity, so that could account for this difference. It is conceivable that training to suppress EMG activity during imagery might inhibit any alpha motoneuron activity (See Requin below). They concluded by agreeing with Frith and Dolan (1997) that »mental imagery reflects the effects of previous knowledge about the predicted sensory effects of the subject’s own actions on sensory processing areas in the absence of sensory input« (Naito et al. 2002, p. 3689).

Rehearsing all the Circuitry

Jeannerod’s experiments produced different evidence on this question. He found that »(...) even if you are simply imagining the action in terms of its goal, in simulating it you also rehearse all the neuronal circuitry. (...) if you examine the brain activity during motor imagination, you will find activation of the motor cortex, the cerebellum, etc.« (Gallagher & Jeannerod 2002, p. 14). This includes the spinal motoneurons. »Insofar as the sensitivity of neuromuscular spindles is under the control of gamma motoneurons, the increase in excitability of the T-reflex, but not of the H-reflex, suggests a

selective increase in gamma motoneuron activity during mental simulation of a movement« (Jeannerod 1999, p. 7).

There are several approaches to determine if the body is involved in motor imagery. The increase in the activity of the EMG is often used. The absence of EMG increase is not indicative of a lack of potentiation of the alpha motoneuron. *There are many influences on the excitability of the alpha motoneurons included in the muscle stretch reflex path.* (Intraspinal, cutaneous, or autonomic input is not being considered here). Fadiga found that corticospinal excitability was specifically modulated by motor imagery in a magnetic stimulation study, recording motor evoked potentials in the muscles (Fadiga 1998, pp. 147–158). Corticospinal excitability refers to the excitability of alpha motoneurons stimulated by cortical neurons, and this is manifested in an increase in EMG activity. Was the increase due to gamma motor stimulation to the muscle spindle leading to more proprioceptive stimulation of the alpha motoneurons, or due to direct alpha stimulation? There are several other reports of an increase of EMG activity in muscles involved in the imagined motor act (Porro et al. 1996, p. 7696; Jacobson 1930; Wehner et al. 1984; Harris & Robinson 1986). Some studies have not shown an EMG increase. The results of the studies can reflect differences in consciously preparing a prescribed movement, motor imaging, and mental simulation, and in how the activity is studied. »*During preparation there is concurrent massive inhibition of the alpha motoneurons*«, which »prevents any premature triggering of action« (Jeannerod 1997, p. 118; Requin et al. 1977, pp. 139–174). This can explain the absence of EMGs, H-reflex changes, and motor-evoked potentials in some of the studies (Naito et al. 2002, pp. 3683–3691; Kasai et al. 1997, pp. 147–50). Jeannerod found that the inhibition occurring with *simulation* is less intense, and there is only a »partial block of the selective fusimotor activity«.

Selective Fusimotor Activity

Fusimotor is the same as gamma motor (*L. fusus*, a spindle). Selective refers to activation of fusimotor neurons without simultaneous alpha motor activation. Prochazka proposed that »the fusimotor system plays a role independent of the alpha motoneuron system, associated with arousal and expectancy« (Prochazka 1989, pp. 281–307). Taylor recorded a spindle afferent from a jaw closing muscle in a chronically prepared cat while it was lapping milk. It became satisfied and stopped. After »a short pause the animal took interest in

the milk again and there ensued a period of rhythmically modulated spindle discharge without EMG or jaw movement before lapping recommenced (...) Evidently the central pattern generator started working and sending an output to the (static) *fusimotor neurones before the excitability of the alpha motoneurons was sufficient to make an overt expression of the rhythm*« (Taylor, Durbaba & Rodgers 1995, p. 374).

Gandevia and others in 1997 recorded muscle spindle afferents directly during mental rehearsal of movements. They found that no spindle activity occurred unless there was increased EMG activity. »Mental rehearsal did activate alpha motoneurons, and if this was sufficiently strong, the skeletomotor discharge was accompanied by recruitment of spindle afferents« (p. 264). They theorized that liminal contractions occurred without overt movement, and that this involved unintentional performance of the planned motor task. They concluded that there was no selective fusimotor activation during imagined movement. »Anticipation« is associated with changes in gain of spinal reflexes and muscles are often tensed unintentionally in preparation for the command signal to move« (ibid., p. 265; also see Burke 1980).

Ascending Proprioception during Peripheral Inhibition

So we have evidence of reference to the body for both gamma and alpha. What about afferent feedback from the body of this reference? It is possible that the central stimulation of the gamma motoneurons occurs with concurrent pre-synaptic inhibition of the proprioceptive afferent synapses *with the alpha motoneurons* (to prevent premature action). There are also spindle afferent fibers synapsing with interneurons in the spinal cord, which synapse with somatosensory tracts to the brain. *I propose that these would not be inhibited.* The differential control of collaterals of sensory fibers by GABAergic interneurons results in varying levels of synaptic effectiveness (Rudomin 2002, p. 167). GABA is a neurotransmitter released by most presynaptic terminals. This proprioceptive feedback to the network originating the gamma motor stimulation can be the basis for the organism being aware of how it is preparing for the intended movement via the body-loop through the muscle spindles. Gallagher has proposed that somatic proprioception, in its most typical form, provides a sense of ownership for the body and its movements (2003). This is a pre-reflective, *non-perceptual bodily awareness*. It refers to the *subjective experience* of ownership of embodiment. He is referring to posture and movement, but I find that his analysis fits the process of preparing to move.

No Motor Imaging without Involving the Body

It is possible that the artificial circumstances of experimental studies asking for motor imaging result in very minimal emotional motivation, particularly when required to relax. In this case, there would be no proprioceptive afference from the body loop, so that the body would be by-passed for this mode, except for visual and vestibular. The as-if body loop would still operate.

In discussing how covert actions simulate actions, Jeannerod says: »(...) activation of the motor cortex and of the descending motor pathways seems to fulfill several critical functions. First, this activation contributes to generating corollary signals that propagate upstream to parietal and premotor cortex. This mechanism would allow evaluation of the potential consequences of the future action. It could also provide the subject with information for consciously monitoring his (simulation states) and realizing that he is the *agent of this covert activity*, in spite of absence of overt behavior« (Jeannerod 2001, p.108; emphasis added). What is the source of this »information for consciously monitoring?« The phrase »descending motor pathways« could refer only to the subcortical motor nuclei of the thalamus and basal ganglia or also to the pathways descending to the gamma motor neurons, which would generate afferent signals from the muscle spindles. The innervation of the gamma motoneurons occurs over four pathways: corticobulbospinal, rubrospinal, reticulospinal, and vestibulospinal. The corticobulbar fibers synapse in the red nucleus and motor areas of the reticular formation in the brain stem, where the rubrospinal and reticulospinal tracts arise (Kingsley 2000, pp. 241–7). The vestibulospinal tract originates in the vestibular nuclei of the brain stem. Their various effects are facilitatory or inhibitory of the alpha and gamma motoneurons. When he realizes that »he is the agent of this covert activity«, we suggest that he experiences the activity as a motor intention.

The organism prepares to interact by activity in the entire motor system, including the gamma motoneurons to the muscle spindles. The organism is also directly preparing the alpha motoneurons for the action as the final common pathway. This exemplifies the hierarchy of potentiation described above by Gallistel. All of the supraspinal networks that influence the gamma motoneurons may also affect the alpha motoneurons' excitability. Most of them act through interneurons, allowing for integration of influences.

Conclusion

The primary importance of the motivation originating from the subcortical emotional circuits rests on the fact that this is the area responding to the biological needs of the organism. These are the value-generators. »Without emotion allowing and informing a central representation of value, executive and attentional functions are collapsed at their base, as are personal meaning and any viable image of agentic active self (...)« (Watt 1999, p. 193). The activities of the higher levels of the brain are organized around the emotional motivation originating here. Speaking of the needs and values of the organism, it might be well to add that one of the emotional neural circuits that Panksepp delineates deals with the social needs for bonding, sex, and nurturance.

Ellis and Newton proposed that when the three elements described above interact in a certain way, they are inevitably accompanied by consciousness. »If the organism's knowledge of its environment is to involve a ›felt‹ dimension, in the sense that there is ›something it feels like‹ to have a state of consciousness, the conscious processing must first flow from an emotional process within the organism, which pre-exists any particular input, and puts its qualitative stamp on each selected input« (Ellis & Newton 1998, p. 431). The phrase »interact in a certain way«, of course, raises many intriguing questions.

The sense of self as *covert* agent originates in the subcortical area centered on the periaqueductal gray. The primitive emotional circuits motivate the behavior by potentiating a movement interaction with the affordance. It is proposed that this potentiation stimulates the gamma motoneurons to the muscle spindles in the muscles and the alpha motoneurons themselves. The resulting proprioceptive activity is fed back to the network of origin, which leads to an awareness of self as generating the potentiation. This aspect of the sense of self thus depends on somatosensory feedback. »Proprioceptive awareness thus provides an immediate experiential access to my pre-reflective, embodied self (...)« (Gallagher & Marcel 1999, p. 21).

Appendix

The muscle spindles are tiny sensory receptors embedded in the skeletal muscles. They sense the steady-state length of the muscle as well as dynamic changes in length and tension. When the muscle is stretched, the spindle is also stretched, and the sensory nerve activity increases. When the muscle contracts, the spindle length decreases, and the sensory nerve activity decreases (unless overridden by the central nervous system – see below).

There is, however, a unique feature of this sensory receptor. It contains tiny muscle fibres (called intrafusal). When the gamma motor nerve to the spindle causes the intrafusal muscle fibres to contract, the spindle's sensitivity to stretch increases. This has important ramifications. Even though the muscle itself remains at the same length and is not stretched, the gamma motor stimulation has increased the stimulation of the sensory nerves just as though the muscle had been stretched. *There is no movement of the muscles, but there is increased proprioceptive activity* (Kingsley 2000, p. 217 and Matthews 1982). When this occurs, impulses travel up the muscle afferent nerves to the spinal cord. There they synapse with the alpha motoneurons that can contract the muscle itself with added stimulation from the brain. The increase of stimulation from the muscle spindles exerts a powerful facilitation of these neurons (they are more sensitive to stimulation). The muscle tone is increased (Taylor & Prochazka, 1981; Taylor et al. 1995). The gamma and alpha motoneurons both originate in the spinal cord and send axons to the muscles. Their activity is influenced by supraspinal and propriospinal activity, by cutaneous afferent and autonomic input (Gladden 2000, p. 213), and by interneurons in the spinal cord. The subject's motor set alters the response to these influences. The muscle afferent nerves stimulate neural tracts going to the brain (Fig.1). The central stimulation of the gamma and alpha motoneurons can be independent or integrated. The central nervous system stimulation of the gamma motoneurons may precede the alpha stimulation, thus facilitating their activity, or the gamma stimulation may increase simultaneously with the alpha when a muscle contraction is initiated (Kingsley 2000, pp. 221–223).

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About the Author

Anton Lethin has been a research fellow in neurophysiology at Yale, an associate clinical professor of pediatrics at the University of California, San Francisco, and a Bioenergetics mind-body therapist. He has published articles on a variety of topics including physiology, emotion, and embodied intentionality.

Anton Lethin
300 Moncada Way
San Francisco, California 94127
a.lethin@att.net